A STUDY OF DEVELOPMENT IN THE GENUS CORTINARIUS

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The genus *Cortinarius* has always been one of particular interest to me on account of the exquisite beauty of its coloration and, in certain species, the peculiar delicacy of its cobwebby veil. It seems strange that a structure as fragile as the latter could be at the same time so persistent, continuing, as it does, until the fruit body has pushed its way well up through the hard particles of soil. It was, therefore, with considerable delight that, while looking for material for morphological study, in company with Professor Atkinson, we ran across *Cortinarius distans* and *Cortinarius cinnamomeus* in all stages of development. This collection, with that of three other species, previously fixed and embedded by Professor Atkinson, furnished the material for the study described in this paper.

The development of *Cortinarius* has never been studied. Kauffman,[1] in his systematic work on the genus, pointed out the need of a more thorough study of the young stages, in order to determine the exact origin of the universal veil and the cortina. Since this work was published, the confusion in regard to the veils in a number of the Agaricaceae has been cleared away by the studies of Atkinson concerning the homologies of the veil in species of *Agaricus*[2,3,4], *Lepiota*,[5] *Amanitopsis*,[6] and *Coprinus*.[8] In the light of this recent work, it becomes important that other species of the family *Agaricaceae* be

[1] Kauffman, C. H. The genus Cortinarius, a preliminary study. Bull. Torrey Club **32**: 301–325. 1905.

[2] Atkinson, G. F. The development of *Agaricus campestris*. Bot. Gaz. **42**: 241–264. pls. 7–12. 1906.

[3] Atkinson, G. F. The development of *Agaricus arvensis* and *A. comtulus*. Amer. Journ. Bot. **1**: 3–22. pls. 1, 2. 1914.

[4] Atkinson, G. F. Morphology and development of *Agaricus rodmani*. Proc. Amer. Phil. Soc. **54**: 309–343. pls. 7–13. 1915.

[5] Atkinson, G. F. The development of *Lepiota clypeolaria*. Ann. Mycol. **12**: 346–356. pls. 13–16. 1914.

[6] Atkinson, G. F. The development of *Amanitopsis vaginata*. Ann. Mycol. **12**: 369–392. pls. 17–19. 1914.

investigated in regard to the homologies of their veils and the manner of formation of their gills, especially since the exact origin of the latter in the genus *Coprinus*[7,8] has recently become a matter of some controversy. This investigation was accordingly undertaken in order to determine (1) the method of development of the universal and partial veils; and (2) the exact origin of the gills in these five species of *Cortinarius*.

Collection and Preparation of Material.—The material for this investigation was all obtained in the vicinity of Ithaca, N. Y. *Cortinarius distans* Peck and *C. cinnamomeus* Fries were collected in the woods on the south side of Taughannock Gorge, August 27, 1914. The young fruit bodies were dug from rich leaf mold, through which the spawn was running, in the vicinity of mature plants. They were immediately fixed in medium chrome-acetic acid. *C. armillatus* Fries, *C. lilacinus* Peck and *C. anfractus* Fries were collected in a similar manner by Professor Atkinson, the former from the moor at Malloryville, N. Y., and the two latter from the woods by Michigan Hollow swamp near Danby, N. Y., in September, 1914.

The material was dehydrated, cleared in cedar oil and embedded in 52° paraffine. About 300 slides were made of the five species. Sections were cut 5 and 6 microns in thickness. Basic fuchsin proved a most satisfactory stain for *C. cinnamomeus* and *C. distans*, but would not take well in the tissues of the other plants. *C. anfractus* stained well with carbol fuchsin, but *C. lilacinus* proved most resistant, even to this heroic treatment. At the suggestion of Professor Atkinson, a little experimenting was carried on to determine the effectiveness of tannic acid as a mordant, after the sections were fixed to the slide. This substance has generally proved very satisfactory in the case of fungi, when used at the time of killing. It was found that, if the slides were allowed to stand in a 1–2 percent solution for a half-hour and then washed for fifteen minutes in running water, they took most readily the fuchsin and methyl blue stains without precipitation. Sections of *C. lilacinus* and *C. armillatus* were stained in this manner as well as with iron-alum haematoxylin. The fuchsin, however, proved far superior to the others for the photographing.

[7] Levine, M. The origin and development of the lamellae in *Coprinus micaceus*. Amer. Journ. Bot. **1**: 343–356. pls. 39, 40. 1914.

[8] Atkinson, G. F. Origin and development of the lamellae in Coprinus. Bot. Gaz. **61**: 89–130. Diagrams I–VI. pls. 5–12. 1916.

Cortinarius anfractus

(Figs. 1–18)

Primordium of the Basidiocarp.—The earliest stage obtained of *C. anfractus* was a tiny button $\frac{1}{4}$ mm. in length and somewhat conical in shape. But for its attachment to slightly larger fruit bodies, it might easily have been overlooked on account of its diminutiveness (fig. 1). The tissue is homogeneous in character, being composed of densely interwoven hyphae, averaging 1.6 μ in diameter. In certain places on the surface, there is some evidence of a thin, deeply stained external layer, the protoblem. This name was proposed by Atkinson for the very delicate primary universal veil in *Agaricus campestris*[9,10], which separates early from the pileus in the form of very distinct and delicate floccose scales and never becomes concrete with the pileus, as does the true universal veil or blematogen. Owing to the fact that these buttons develop beneath the soil, and because of the friction in washing, it is not strange that only traces of this layer are found in the young stages.

Differentiation of the Pileus and Stem Primordia.—The first internal evidence of differentiation occurs in fruit bodies of about 1 mm. in length. In the central part of the fruit body there appears a deeply staining growth region, conical in form, leaving on the outside an area of loose ground tissue (fig. 1). This conical growth area is the stem primordium. We may consider the outer region as a portion of the blematogen, homologous to that described by Atkinson in the species of *Agaricus*,[11,12] *Lepiota*,[13] *Armillaria*,[14] *Coprinus*,[15]

[9] Atkinson, G. F. The development of *Agaricus arvensis* and *A. comtulus*. Amer. Journ. Bot. **1**: 3–22. pls. 1, 2. 1914.

[10] Atkinson, G. F. Homology of the universal veil in Agaricus. Mycol. Cent. **5**: 13–20. pls. 1–3. 1914.

[11] Atkinson, G. F. The development of *Agaricus arvensis* and *A. comtulus*. Amer. Journ. Bot. **1**: 3–22. pls. 1, 2. 1914.

[12] Atkinson, G. F. Morphology and development of *Agaricus rodmani*. Proc. Amer. Phil. Soc. **54**: 309–343. pls. 7–13. 1915.

[13] Atkinson, G. F. The development of *Lepiota clypeolaria*. Ann. Mycol. **12**: 346–356. pls. 13–16. 1914.

[14] Atkinson, G. F. The development of *Armillaria mellea*. Mycol. Cent. **4**: 113–120. pls. 1, 2. 1914.

[15] Atkinson, G. F. Origin and development of the lamellae in *Coprinus*. Bot. Gaz. **61**: 89–130. Diagrams I–VI. pls. 5–12. 1916.

Amanitopsis.[16] The loose character of the tissue is due to the less active growth of this region, the hyphae elongating but producing no new elements. As in the case of the species mentioned, the exact limits of this region are impossible to define in the early stages. In the right-hand object of figure 1 this internal growth area has reached the apex of the young fruit body. The upper end of this probably represents the pileus primordium, though there is no evidence of its differentiation from the stem.

It is not until the buttons reach the stage of figure 2 that we can distinguish the separate fundaments of the different regions. At the top of the central growth region, there is differentiated a dome-shaped area, which takes the stain more deeply at its margin. This dome-shaped area represents the fundament of the pileus (fig. 2) and the deeply stained margin, the primordium of the hymenophore. As soon as the latter appears, the fundament of the stem is delineated as that part of the central dense area below the pileus. At the same time the ground tissue between the margin of the pileus and the stem becomes the fundament of the partial veil. From this time on expansion of the fruit body takes place in all directions, particularly in the longitudinal one, and the mesh becomes more and more open (figs. 3 and 4).

The Development of the Hymenophore.—The margin of the pileus fundament (fig. 2) forms an annular zone of very actively growing hyphae, which are becoming very crowded and are turning downward and obliquely outward. They are very rich in protoplasm and contain very prominent nuclei. This annular zone stains deeply and is shown in section in figure 2 as two deeply staining areas one on either side. This annular zone is the fundament of the hymenophore. The hyphae are provided with very sharp ends, thus enabling them to penetrate the ground tissue below the more easily (fig. 10). The hyphae first appear near the stem fundament and as the pileus expands, they are continually being formed at the margin. At the same time, by the branching of the hyphae, new ones are interpolated between the original ones, causing the tissue to become more and more compact.

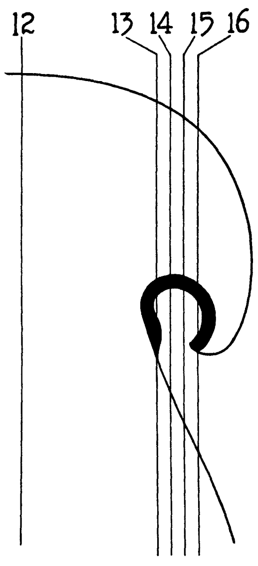
Origin of the Palisade Layer and Gill Cavity.—When the primordium of the hymenophore is first formed, the growth of the hyphae is very unequal and consequently the lower surface presents the very irregular

[16] Atkinson, G. F. The development of *Amanitopsis vaginata*. Ann. Mycol. **12**: 369–392. pls. 17–19. 1914.

appearance shown in figures 3 and 10, and in the tangential section of the same fruit body (fig. 4). Soon, however, as new elements are formed in a centrifugal manner, the zone of the hymenophore near the stem begins to change its appearance. The ends of the hyphae become more even and stouter, thus forming the dense palisade tissue shown in figures 5, 6, and 7, and in the slightly older fruit body of figures 8, 9, and 11. It is in this stage that we first find evidence of a gill cavity. The palisade layer becomes very crowded on account of the broadening of the hyphae and the interpolation of new elements. At the same time the growth of the pileus becomes strongly epinastic. These two factors together exert considerable tension on the hyphae of the ground tissue, with the result that they finally break and leave a cavity below the palisade layer. The ragged under surface of the latter in these figures is due to the ends of the broken hyphae. Many seem to be able to stand considerable stretching, so that the cavity at first is rather weak. It is, however, important to notice that before there is any evidence of gill formation, there is a well defined, even, palisade layer.

Origin of the Partial Veil.—We have seen that very early in the life history of the fruit body, the pileus and stem primordia are differentiated by the appearance of a dome-shaped area, growing very actively at its margin and here forming the primordium of the hymenophore. The general region of looser plectenchyma, extending over the pileus, outside the hymenophore and down over the stem primordium, is the blematogen. The ground tissue within this somewhat indefinite zone, lying between the margin of the pileus and the stem fundaments, represents, as before noted, the partial veil. As the plant matures, the upper part of the pileus fundament grows into and becomes consolidated with the blematogen, which forms here a firm cortex. At the sides, however, the blematogen shows a more or less duplex character (figs. 3 and 5). There is a very thin but firm outer layer, which stains very deeply and is composed of two or three rows of parallel or slightly interwoven hyphae with large diameters. Within, the blematogen is very loose and delicate and is exactly similar to the tissue of the partial veil. This double character may be distinguished even on the upper surface of the pileus margin (figs. 3, 5, and 8), where the outer layer merges into the cortex of the fruit body, quite similar in its composition. This rind is very persistent, retaining its integrity until after the gills are fairly developed (fig. 17). It is

quite conspicuous even to the naked eye. As the plant matures, new elements appear to be formed at the margin of the pileus. These extend across, below the gill cavity, to the stem. Whether or not the cortina has its insertion on the upper surface of the pileus margin, depends, therefore, on our conception of what the cortina is. *C. anfractus* is placed by systematists in the sub-genus, *Phlegmacium*, one of whose characters is the presence of a partial veil only. We have seen from this study, however, that *C. anfractus* does possess a blematogen outer layer, which is homologous with a universal veil, but is not clearly differentiated from the pileus as such. The marginal or partial veil, strictly speaking, consists only of the ground tissue, between the stem and pileus margin and the new elements added by growth. As the term cortina is a special one, applied chiefly to the cobwebby veil of this genus, it should probably include all the fibers of the veil and thus may be considered as consisting of both blematogen and partial veil tissue.



Text-fig. 1. Diagram to show plane of sections shown in figures 12–16, plate IX.

Origin of the Lamellae.—The first evidence of gill formation occurs in specimens of about 3.5 mm. diameter. Figures 12–16 show a series of longitudinal sections, cut parallel with the axis of the stem, in the positions represented by the corresponding numbers in the diagram of text-figure 1. Let us first examine section 14, from a plane through the center of the gill cavity, recalling, as we do so, that the hymenophore always develops centrifugally and in consequence, the oldest stages will be nearer the stem and the youngest nearer the margin of the pileus. The latter portion of the hymenophore is still in the primordial state (fig. 16) showing the irregular, sharply pointed hyphae. As we approach the stem, we pass by even palisade tissue to the young gill salients (fig. 15) growing down into a now well defined annular cavity. If we examine them in greater detail (fig. 18), we see that they are formed by the dense crowding of the palisade layer, accompanied by an elongation of the subadjacent hyphae in regularly

spaced radial areas. The palisade layer is thus pushed out into folds, which allows room for the expansion of the ends of the hyphae, now considerably swollen. Subadjacent to the stratum of young salients, there appears a thin growth zone, very conspicuous on account of its abundant nuclei. In the center of each gill, it extends down into the trama, but between the gills it remains as a thin layer[17] (figs. 13–15, 18). It maiks the boundary of the pileus and the hymenophore and probably represents the region where cleavage takes place in such forms as *Paxillus*, in which the hymenophore separates readily from the flesh of the pileus. As we approach the stem, we find the salients more mature. The median section of figure 12 shows that the hymenophore, when cut radially, is more or less crescent shaped, due to the inrolling of the edge of the pileus and the decurrence of the gills along the slanting surface of the stem. As the knife passed through the plane represented by line 13, it cut through the junction of the decurrent gills with the stem and nearly perpendicular to their direction of growth. For this reason, the space between them, a part of the main gill cavity, appears as a little pocket. In a similar manner, the peculiar appearance of figure 16 may be explained. The curving inward of the margin of the pileus caused the hymenophore primordium to be cut twice.

Structure of the Pileus and Stem.—The pileus and stem are both composed of a very homogeneous and yet firm tissue, containing very large air spaces. Toward the outside of the pileus, the tissue becomes more and more dense until it passes into the firm cortex, spoken of above. On the outside of the cortex, we frequently find large, thick-walled hyphae undergoing disintegration and giving the pileus surface the viscid character common to this sub-genus. In the cortical region of the pileus, the hyphae are filled with large oily drops, remaining unstained. At the apex of the stem the tissue is very dense, but it becomes more and more open towards the base, thus providing for aeration of the tissues. In this region also the hyphae are stouter and have thicker walls than those above near the pileus. The general direction of the hyphae in the stem is longitudinal or slightly oblique. They are somewhat interwoven. On the

[17] This recalls the distinct zone from which the hymenophore originates in *Polyporus fumosus* as described by Miss Ames (p. 225, figs. 38, 39). See Ames, A. A consideration of structure in relation to genera of the Polyporaceae. Ann. Mycol. 11: 211–253. pls. 10–13. 1913.

outside of the stem, they are slender and dense, forming a very firm outer supporting layer.

CORTINARIUS CINNAMOMEUS

(Figs. 25–50)

Early Stages of Development.—*Cortinarius cinnamomeus* develops in a manner very similar to that of *C. anfractus*, although there is considerable difference in the appearance of their tissues, that of this species being more dense in its character than that of the preceding. The earliest stage examined is represented by figure 25, from a section of a button about 2 mm. × 1 mm. in size. This has already differentiated sufficiently to show a dense dome-shaped fundament of the pileus and that of the stem below and it is quite possible that earlier stages would show the stem fundament differentiated first as a conical area, as described for *C. anfractus* and for the other species described in this paper. The hyphae of the pileus fundament average about 1.6 μ in diameter but in the lower part of the stem and in the veil region they reach two or three times this size. The pileus primordium lies very near the surface, leaving only a very narrow thin zone of blematogen. The latter is composed of large hyphae with diameters of 4 or 5 μ. They are somewhat interwoven and are arranged more or less radially over the surface of the pileus, excepting in the hymenophore region, where they are very nearly parallel to the surface. This blematogen layer is retained by the plant until maturity and accounts for the fibrillose nature of the surface of the pileus, a distinguishing characteristic of the sub-genus *Dermocybe*, to which *C. cinnamomeus* belongs. It never separates as a universal veil but is partly worn off in the form of scales, as the fruit body pushes through the soil (figs. 32, 39, 44). The lost fibrils appear to be continually replaced by outgrowths from the surface of the pileus. The marginal veil never becomes very strongly developed. It receives new elements from the margin of the pileus (figs. 28, 30), but it retains its loose floccose nature. The large open mesh provides a very free communication for air with the outside.

The Development of the Hymenophore.—Simultaneous with or soon after the formation of the pileus fundament takes place, an internal annular zone of rapid growth appears at its margin and represents the beginning of the hymenophore. This primordial stage is followed by

the development of the palisade layer (figs. 27, 28, 29, 30, 31). Owing to the weakness of the fibers of the ground tissue, a strong gill cavity makes its appearance early (figs. 29, 30). In figures 32–38 is shown a series of sections of the earliest fruit body to show the gill beginnings. Excepting for slightly more irregularity of the salients, their development is quite similar to that of *C. anfractus*. In this specimen the gills are merely adnate to the stem and, in consequence, do not show the pockets at the junction of the stem, which we saw in *C. anfractus*. There is considerable variation in this respect among individuals of the same species. The older specimen, shown in figures 39–43, has decurrent gills and in consequence we find the pockets present. This series of sections is interesting on account of the beginning of the secondary gills. The primary ones have already reached a considerable degree of development, when the second series begin to appear (figs. 45–49). As the pileus expands, the primary salients are pushed farther and farther apart by the intercalary growth and finally the new salients begin to form. At first the surface between the original gills is even. Then the ends of the hyphae become swollen and there is considerable crowding, especially next the primary gills (fig. 45). This is followed by an elongation of the hyphae, carrying the gill down into the cavity. The hyphae in the central portion grow straight downward, but their dense crowding and swollen ends cause the others to turn outward. In the course of development, many new hyphae are interpolated between the old, contributing also to the increase in length. The terminal cells of the hyphae take the stain with difficulty, showing that the greater activity in growth is behind the tips, where the stain is deep and the nuclei abundant. We find in this species the same narrow deeply staining growth region subadjacent to the salients and extending down into their trama (figs. 40–43, 48, 49), that we found in *C. anfractus*. Figure 43 may need a word of explanation. The section was cut somewhat obliquely, so that it passes through the gill cavity on one side, but through the margin of the pileus on the other. It thus passes perpendicularly to the direction of growth of the gill salients on one side, thereby forming pockets as on the stem. This results from the strongly incurved margin of the pileus (see figs. 40–42). In figure 50 is represented a section of the hymenophore from a fruit body having mature gills.

Cortinarius armillatus

(Figs. 19–24)

Cortinarius armillatus and *Cortinarius distans* are of especial interest on account of the fact that both belong to the only subgenus, *Telamonia*, described as possessing a universal veil. *C. armillatus* derives its name from the fact that, as the veil breaks away from the margin of the pileus, it is left on the stem in a series of rings. The material was not found in great abundance but represents the most critical stages of development, except the origin of the hymenophore. The youngest stage (fig. 19) already shows a differentiation into three regions. In the center there is a region of active growth, conical in shape, which probably represents the stem fundament. This is surrounded by a zone of ground tissue, on the surface of which is a layer of large thick-walled hyphae. The latter is probably not a protoblem, evidence of which shows in the older fruit bodies, but is perhaps due to changes in the hyphae, caused by some substance in the substratum with which it came in contact. The older specimen, represented in figure 20, shows a considerable increase in the central growth zone, which now extends upwards nearly to the apex of the young basidiocarp. Progression of the growth area of the stem fundament upward gives rise to the pileus fundament which is surrounded laterally by loose ground tissue and blematogen, there being evidence of a slight but broad constriction between pileus and stem fundament. This method of differentiation of stem and pileus fundament is like that described by A. Möller[18] (p. 70) for *Rozites gongylophora*, and by Atkinson[19] for *Lepiota cristata* and *seminuda*.

On the outside is a very delicate layer of fibrils, which in all probability here represents a true protoblem. It is present in all the older stages where we find very delicate fibrils or scales gradually being shed by the plant. For this reason, we may assume that it is also present in the early stages, but was lost from the button of figure 19 during the preparation processes. The zone just within represents the blematogen, a region very indefinite in the young stages. As the plant becomes older, the boundaries of the blematogen become more distinct

[18] Möller, A. Die Pilzgärten einiger südamerikanischer Ameisen. Bot. Mittheil. Trop. 6: 1–127, figs. 1–4. pls. 1–7. 1893.

[19] Atkinson, Geo. F. The development of *Lepiota cristata* and *L. seminuda*. Proc. 20th Anniversary N. Y. Bot. Gard.

(figs. 21 and 22) until, in the mature stages, it becomes a very definite area. Its duplex character shows even more distinctly here than in *C. anfractus*. The outer layer is continuous completely over the surface of the pileus, the gill cavity and the upper part of the stem. It is considerably firmer than the floccose portion within, which extends from the upper surface of the pileus margin to the stem, outside the partial veil. The latter is very fragile and as the epinastic growth of the pileus takes place, the hyphae are considerably stretched and become united in strands (fig. 23). The partial veil gradually breaks loose from the pileus margin and, together with the portion of the blematogen outside with which it remains in contact, is torn apart by the elongating stem so that the series of delicate rings, above described, are left around the stem. The stages of early development of the gills are lacking but figures 21 and 22 show that they are preceded by a palisade layer and extensive gill cavity. Figure 24 represents a later stage of the gills and shows the origin of a forked gill, by means of a secondary salient growing out at the base of a primary gill.

Cortinarius distans

(Figs. 63–69)

A few photographs of *Cortinarius distans*, also belonging to the sub-genus *Telamonia*, are shown in figures 63–69. These were chosen to illustrate the character of the veil and the method of development of the gills. A very distinct blematogen layer covers the fruit body. Its hyphae are characteristically large and generally radial in their arrangement over the apex of the fruit body, but become nearly parallel at the sides. They take the stain very lightly. The blematogen soon breaks into scales and becomes easily removed, exposing the surface of the pileus, made up of very firm pseudoparenchymatous tissue (fig. 69). The pileus retains its conical shape as it pushes through the soil and on this account, the blematogen first disappears from the apex and much later at the margin of the pileus. Its floccose character is shown in figure 64, an enlargement of figure 63. On account of the scaling off of the outer layers, it was not determined whether or not the blematogen was originally duplex.

The method of gill formation is like that of *C. anfractus*, with the exception that the salients are broader and more widely distant, resulting in a triangular gill at maturity. On account of this feature, the plant has received its name of *C. distans*.

Cortinarius lilacinus

(Figs. 51–62)

The sub-genus *Inoloma*, to which *C. lilacinus* belongs, is characterized by the presence of a large bulbous base to the stem, a feature which in some species becomes extremely well developed. Before there is any external sign of differentiation, a good-sized tubercle is formed (4 × 5 mm.), within which certain changes are taking place. Figure 51 represents a median section of such a tubercle. The tissue is very nearly homogeneous in character, with the exception of a somewhat more dense, deeply staining region within, broadly conical in form, the primordium of the stem. The next later stage (figs. 52, 53) exhibits a considerable advancement in development. The whole of the lower part of the tubercle has become very dense and compact. Above, the hemispherical pileus primordium is marked off from that of the stem by the deeply staining hymenophore fundament. The fibers in the pileus region are similar to those in the stem, are very closely massed together and assume a generally radial arrangement. At the margin, however, they turn strongly downward and here form the hymenophore primordium (figs. 52, 61). Extending over the surface of the pileus and to the sides of the tubercle, is the blematogen, a still rather indefinite region (fig. 52). The gills are formed in the manner described for the other species. An annular cavity appears at about the time of, or just prior to, the formation of the palisade layer (figs. 56, 57), which is very quickly followed by the formation of the young gills. The palisade cells take the stain less easily than the subadjacent tissue and thus the subadjacent region stands out in sharp contrast. As in *C. anfractus*, the latter represents a new area of active growth. It remains as a thin stratum between the gills but when it reaches them, it curves downward and growing very actively forms the greater part of the trama.

On the surface of the fruit body, no definite cortex is formed. Although the pileus and the blematogen becomes consolidated, in the older stages the boundary between the two regions becomes very distinct, owing to the difference in the character of the tissues (fig. 62). The outer layers appear to rub off, as the plant pushes up through the soil, so that a duplex character to the veil is here not apparent. The cortina is made up of the blematogen and the partial veil, to which new elements are added by marginal pileus growth. Practically no

elongation takes place in the stem until all the parts are well organized. In the mature stage shown in figure 62, the fruit body is just beginning to push up from the tubercle.

Summary

1. In the general features of development, these five species of *Cortinarius* are alike. The first differentiation to take place is that of a rapidly growing more or less conical region, the stem primordium, within the fundamental plectenchyma. Growth and progressive differentiation from the apex of the stem fundament gives rise to the pileus primordium. Quickly following the appearance of the pileus fundament there is developed the fundament of the hymenophore, an internal, annular active growth area at the margin of the pileus primordium. Growth is centrifugal. The primordial zone is changed into that of the palisade and this is transformed into the zone of young gill salients. Before the latter make their appearance, a gill cavity of considerable size is formed, by the tensions of the rapidly growing tissues of this region. The tendency to epinastic growth of the pileus margin and the dense crowding of the interpolating elements cause the weak fibers of the ground tissue below to become stretched and finally broken, leaving the cavity.

2. The gills are formed in the following manner: The cells of the palisade layer increase in diameter. This excess of growth is at the same time taken care of by the growth of the subadjacent cells of the hyphae, which elongate in radial rows at regularly spaced intervals. The gill increases in size by the rapid elongation and increase in number of the tramal hyphae, together with an increase in the elements of the palisade and subadjacent layer.

3. In all five species, whether developing a universal veil or not, there is present a blematogen layer. This becomes evident as soon as the fundament of the pileus and hymenophore appear. Its boundaries at first are very indefinite but in general it represents a zone outside the pileus, marginal veil and stem fundaments. Its later disposition varies in the five species. In *C. armillatus* and *C. distans* it enters into the formation of a "universal veil," which separates from the surface of the pileus, but it does not form a true volva, or *teleoblem*. In the other species, it becomes consolidated with the surface of the pileus; in *C. cinnamomeus* breaking up into fibrils which clothe the surface. A very interesting feature of the blematogen is

its duplex character over the margin of the pileus and partial veil. In *C. anfractus* and *C. armillatus* there is developed a firm outer layer, which persists until maturity. This zone is very thin, but extends completely over the upper part of the fruit body. In *C. anfractus* it becomes consolidated with the cortex. The inner portion of the blematogen is much more floccose in character and extends from the upper surface of the margin of the pileus, outside the partial veil, to the stem. In the other three species, *C. cinnamomeus*, *C. distans*, and *C. lilacinus*, the duplex character is not evident, owing perhaps to the early wearing away of the surface. The inner floccose zone is, however, present in all.

4. The marginal veil is developed from the ground tissue lying between the fundaments of the hymenophore and stem, to which are added new elements from the margin of the pileus. The cortina is therefore made up of two elements; 1st, the blematogen on the outside, which extends from the upper surface of the margin of the pileus to the stem; and 2d, the inner threads consisting of the fibers of the marginal veil.

5. One species, *C. armillatus* seems to possess a protoblem. There is evidence of this layer being present in early stages of another species, *C. anfractus*. It is very possible with other methods of fixing and preparation, it might be found in all.

In conclusion, I wish to acknowledge my deep indebtedness to Professor G. F. Atkinson for his kind direction and helpful advice.

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DESCRIPTION OF PLATES VIII–XIII

Figs. 10, 11, 18, 31, 44–49, and 61 were taken with a Bausch and Lomb compound microscope, fitted with a Zeiss 4 mm. ocular and 4 mm. objective. In fig. 64 an 18 mm. oc. and 16 mm. ob. were used. The other figures were photographed by means of an extension camera and Zeiss lenses, figs. 12, 13, 14, 15, 16, 17, 23, 39, 40, 41, 42, 43, with a 35 mm., figs. 52, 53, 54, 55, 58, 59, 60 with a 50 mm. and the others with a 16 mm. Spencer Lens Co. photographic objective.

Cortinarius anfractus (figs. 1–18)

FIG. 1. × 34 diameters. Early stages of three fruit bodies. The one on the left is still undifferentiated, excepting for a darker layer on the outside, which is possibly protoblem. The two older fruit bodies show an area of active growth within, organizing stem and pileus primordia.

FIG. 2. × 34 diam. A slightly older stage. Median section showing the primordia of pileus, hymenophore and stem.

FIG. 3. × 34 diam. Median section of an older stage. The primordial stage is changing into the palisade layer.

FIG. 4. × 34 diam. Tangential section of the fruit body of fig. 3.

FIG. 5. × 34 diam. Median section of a fruit body with the palisade layer well developed. The outer and inner regions of blematogen are shown and the gill cavity is just beginning to form. On the top of the basidiocarp the blematogen has become consolidated with the surface of the pileus and forms a firm cortex.

FIG. 6. × 34 diam. Tangential section of same, near the stem.

FIG. 7. × 34 diam. Tangential section of same, beyond the stem.

FIG. 8. × 34 diam. Older stage, the last to show the palisade layer before the formation of gills.

FIG. 9. × 34 diam. Tangential section of same.

FIG. 10. × 250 diam. The hymenial region of fig. 3, showing the hymenophore primordium on a larger scale.

FIG. 11. × 250 diam. An enlargement of Fig. 8, showing the well-developed palisade layer.

FIGS. 12–16. × 14 diam. A series of sections, showing the various stages in the development of the gills. Fig. 12 represents the median section. The others are all cut parallel to it from the same fruit body.

FIG. 17. × 14 diam. A section of a nearly mature fruit body, showing the persistent blematogen.

FIG. 18. × 250 diam. An enlargement of the young salients of fig. 15 to show the narrow growth zone, subadjacent to the salients. The very abundant nuclei show prominently.

Cortinarius armillatus (figs. 19–24)

FIG. 19. × 34 diam. Youngest stage obtained. The button has begun to differentiate into a central growth region, probably the stem fundament, and an indefinite blematogen. The outside darker layer probably represents modified blematogen.

FIG. 20. × 34 diam. Slightly older stage showing considerable increase in the central growth region. The layer of loose tissue on the outside probably represents a protoblem.

FIGS. 21 AND 22. × 34 diam. Median and tangential sections of a fruit body in which the palisade layer is developed.

FIG. 23. × 14 diam. Median section from a nearly mature specimen, showing the duplex character of the blematogen and the strands of the marginal veil being torn by the tension in growth of the hymenophore and pileus margin.

FIG. 24. × 34 diam. A section showing mature primary gills, and forking caused by the development of secondary salients at their bases.

Cortinarius cinnamomeus (figs. 25–50)

FIG. 25. × 34 diam. Median section of earliest stage obtained. The pileus fundament is evident as a deeply stained saucer-like area near the top of the button. The blematogen consists of the loose tissue upon the surface.

FIG. 26. × 34 diam. A slightly older fruit body, showing the beginning of the hymenophore primordium.

FIGS. 27 AND 28. × 34 diam. Median and tangential sections of an older stage. The palisade layer is in the process of formation.

FIGS. 29 AND 30. × 34 diam. An older fruit body, showing the gill cavity.

FIG. 31. × 250 diam. An enlargement of the palisade layer and gill cavity of Fig. 29.

FIGS. 32–38. × 34 diam. A series of sections at various intervals between the central axis of the stem and the margin of the pileus, showing the origin of the gills. Note the fibrillose character of the pileus surface in fig. 32.

FIGS. 39–43. × 16 diam. Stages in the formation of the gills of an older specimen. The secondary gills are beginning to form.

FIG. 44. × 250 diam. An enlargement of the margin of fig. 39, showing the pseudoparenchymatous cortex and fibrillose surface of the pileus.

FIGS. 45–49. × 250 diam. Stages in the development of a secondary gill. Fig. 45 is nearest the margin. As the sections approach the center, they show progressive stages of maturity.

FIG. 50. × 34 diam. Nearly mature primary and secondary gills.

Cortinarius lilacinus (figs. 51–62)

FIG. 51. × 34 diam. Median sections through a tubercle, showing the differentiation of the stem fundament in the center.

FIGS. 52 AND 53. × 11 diam. Median and tangential sections of an older specimen, showing the pileus, hymenophore and stem primordia.

FIGS. 54 AND 55. × 8 and 11 diam. resp. Older specimen, showing the organization of the palisade layer.

FIGS. 56 AND 57. × 34 diam. The palisade layer and gill cavity, just before the development of the gills.

FIGS. 58, 59 AND 60. × 11 diam. Sections of the youngest fruit body to show gill formation.

FIG. 61. × 250 diam. An enlargement of the hymenophore region of fig. 52, still in the primordial stage.

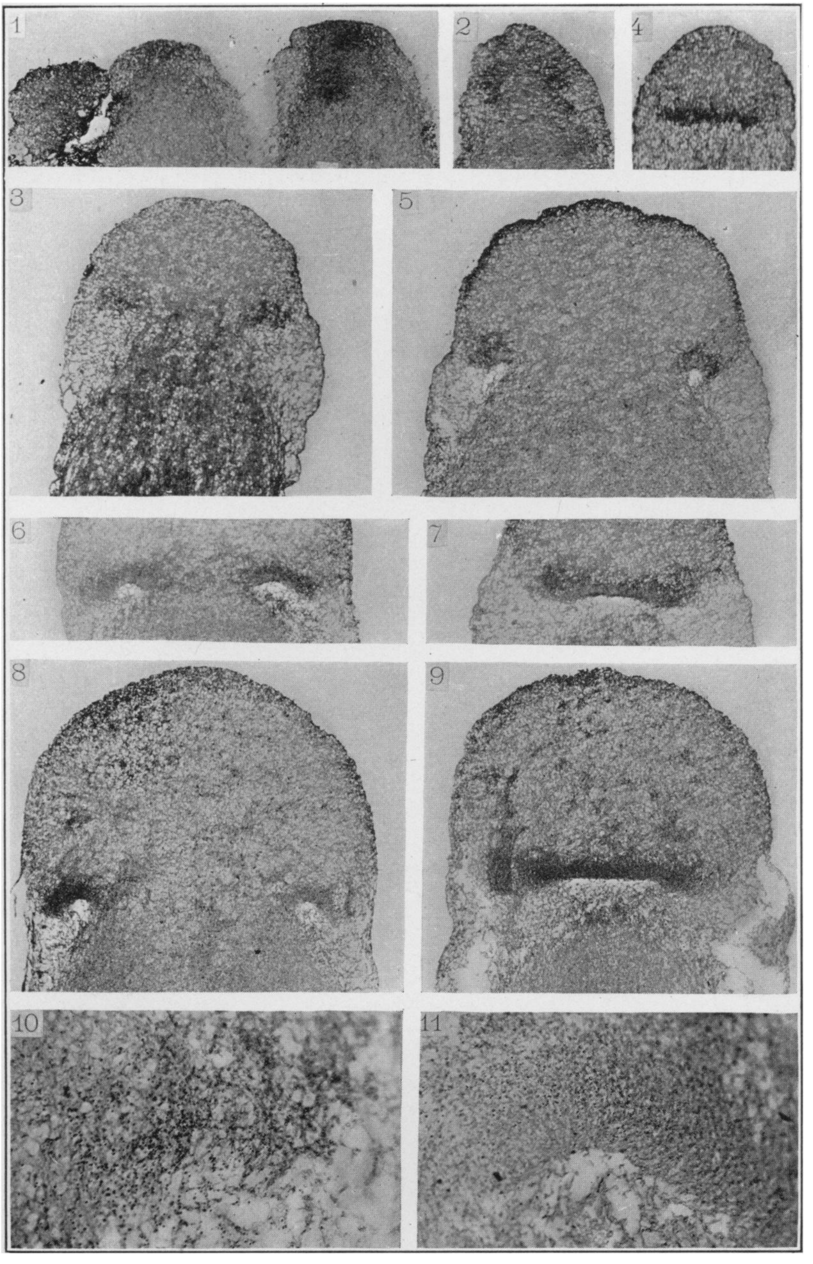
FIG. 62. × 9 diam. A nearly mature fruit body, just commencing to elongate from the tubercle.

Cortinarius distans (figs. 63–69)

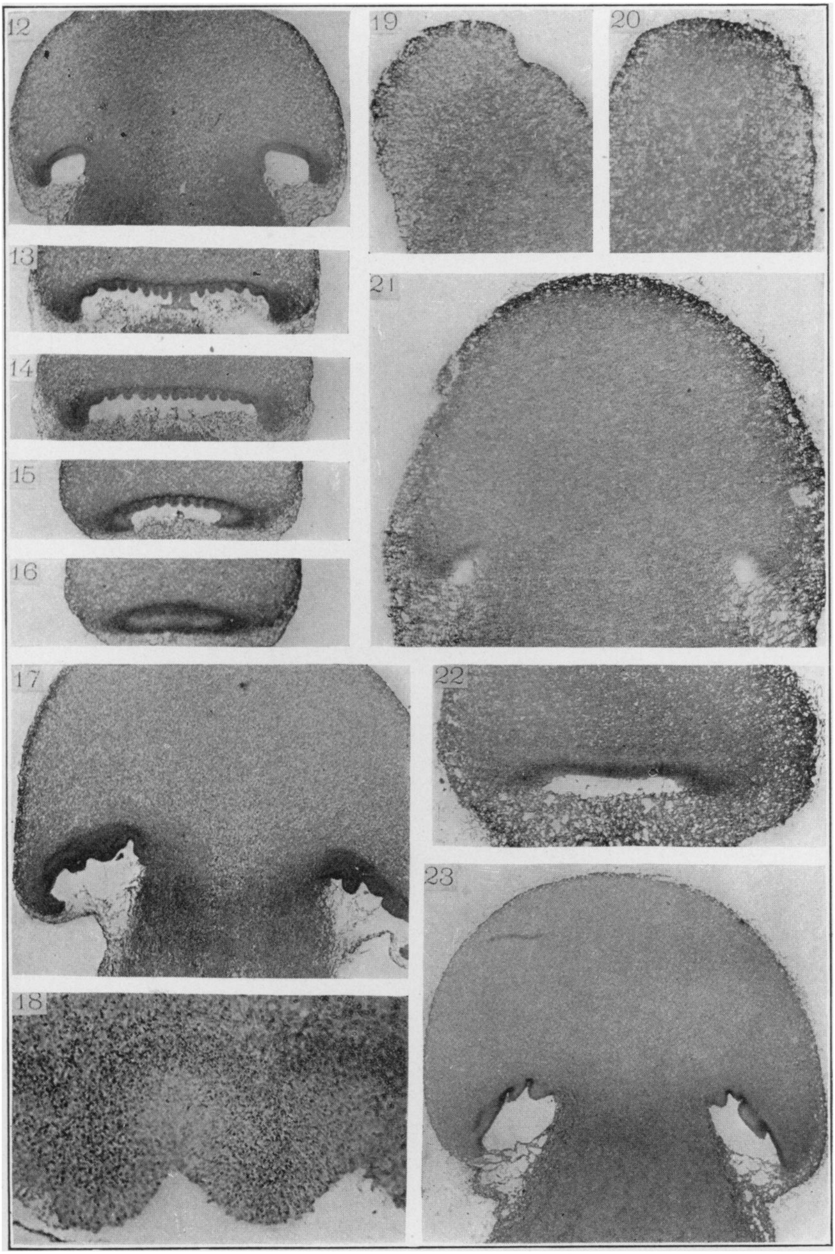
FIGS. 63, 65, 66, 67, 68. × 34 diam. A series of sections showing the development of the gills and the flocculent blematogen, which is rapidly disappearing from the surface.

FIG. 64. × 150 diam. An enlargement of fig. 63, to show the character of the marginal veil, the blematogen and palisade regions.

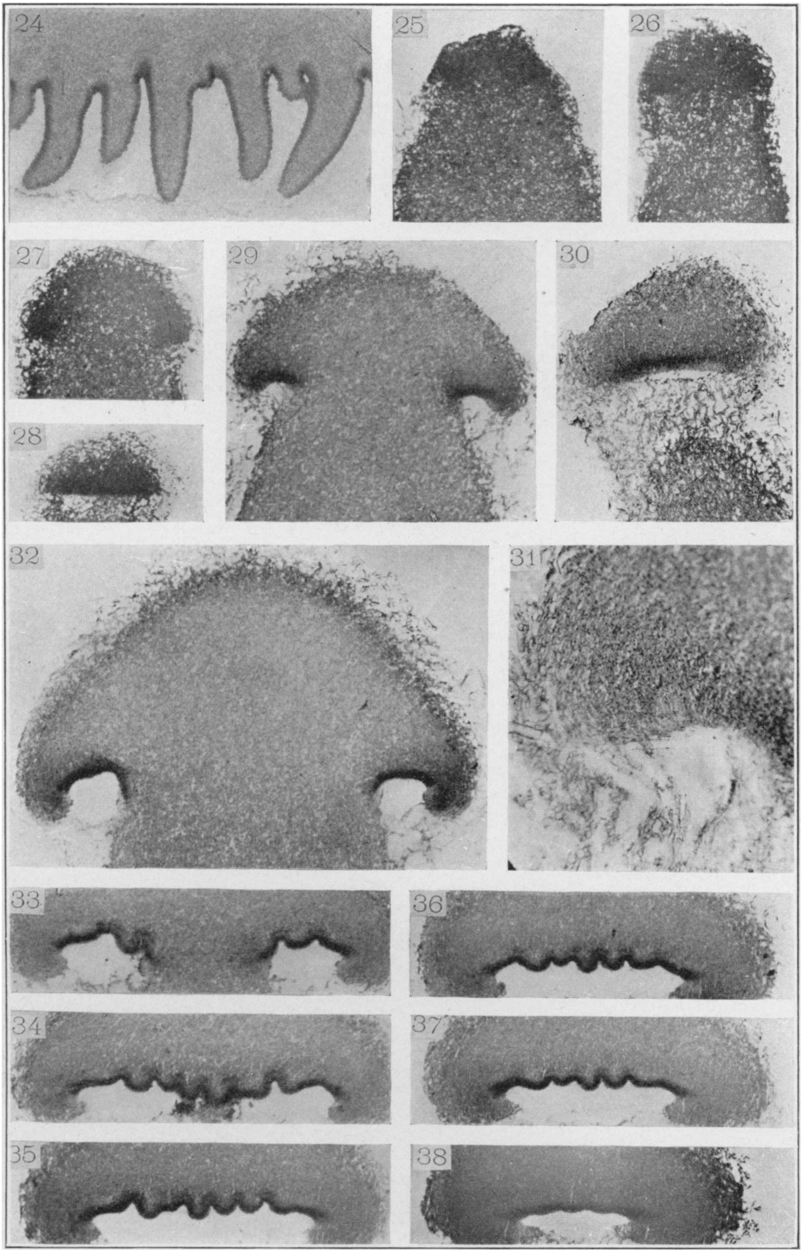
FIG. 69. × 34 diam. Median section of nearly mature fruit body.



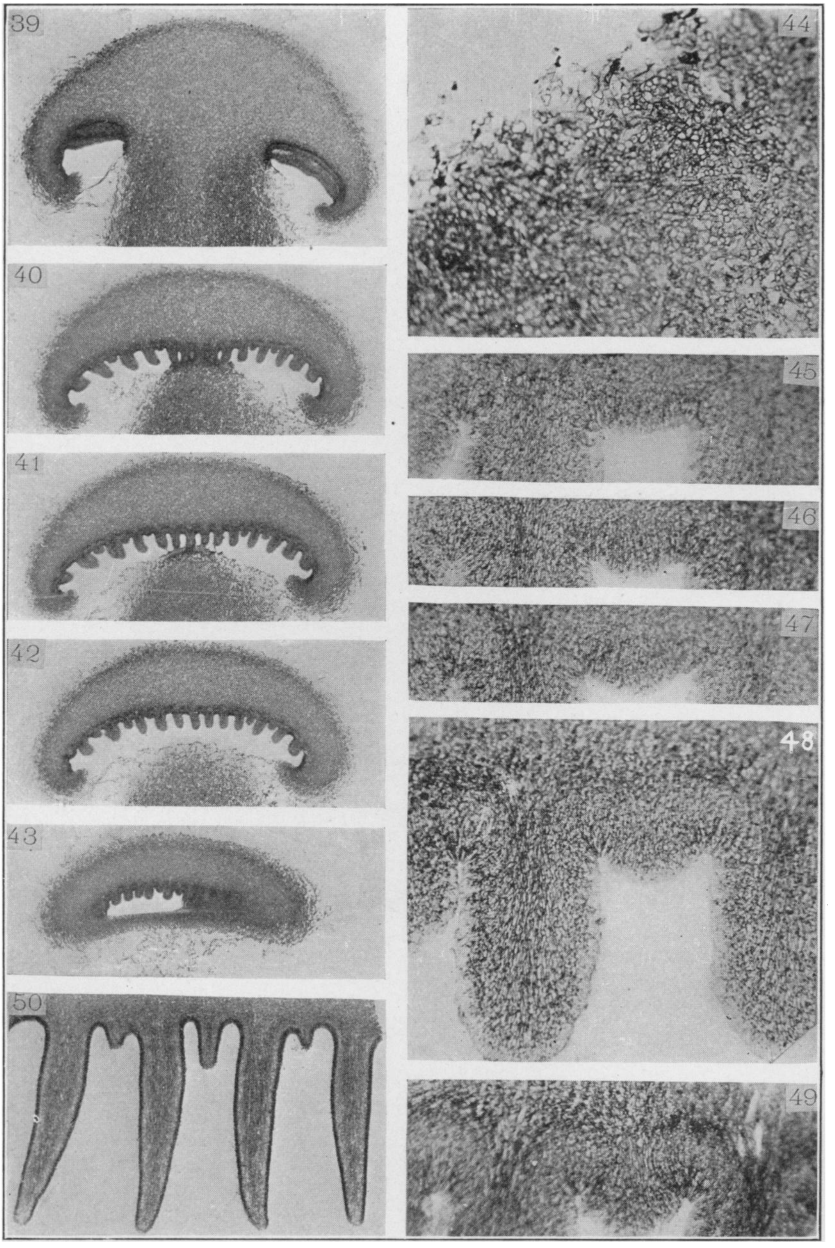
DOUGLAS: CORTINARIUS ANFRACTUS.



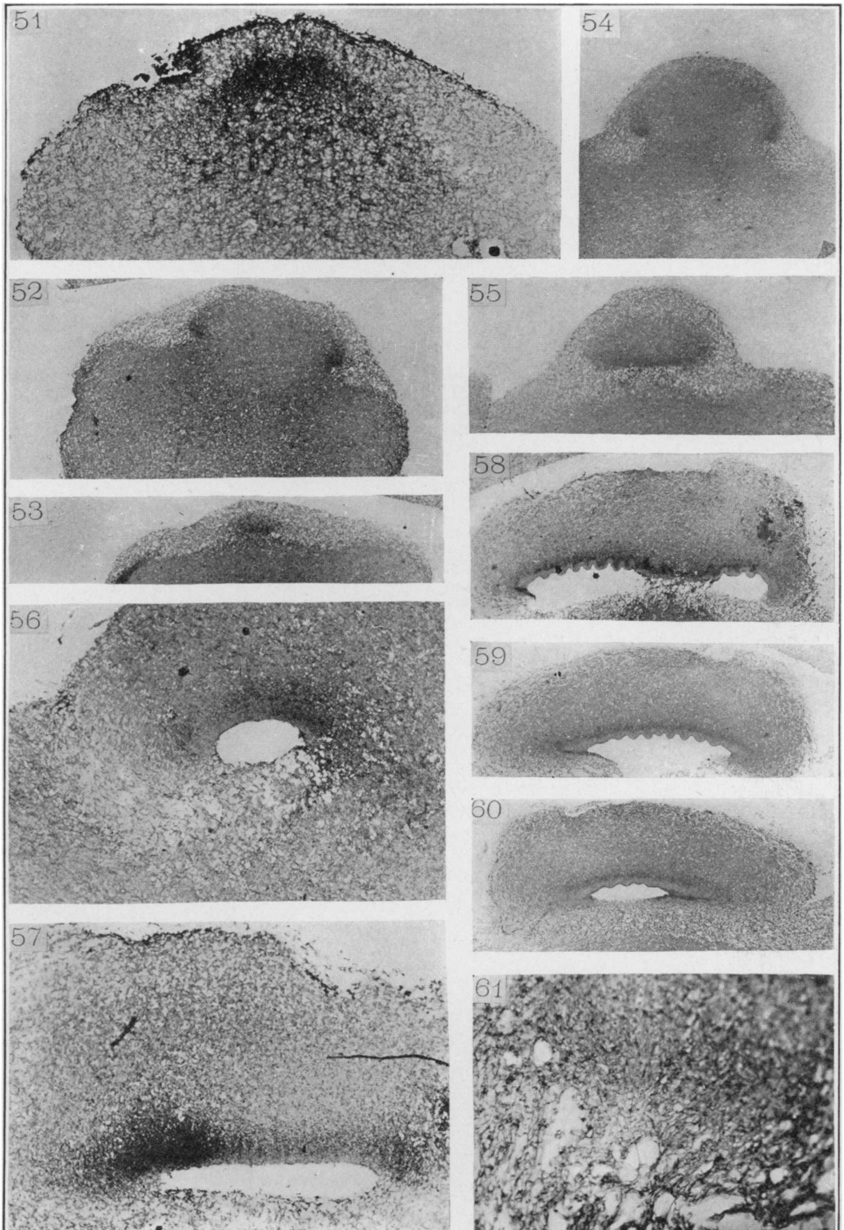
DOUGLAS: CORTINARIUS ANFRACTUS (12–18); C. ARMILLATUS (19–23).



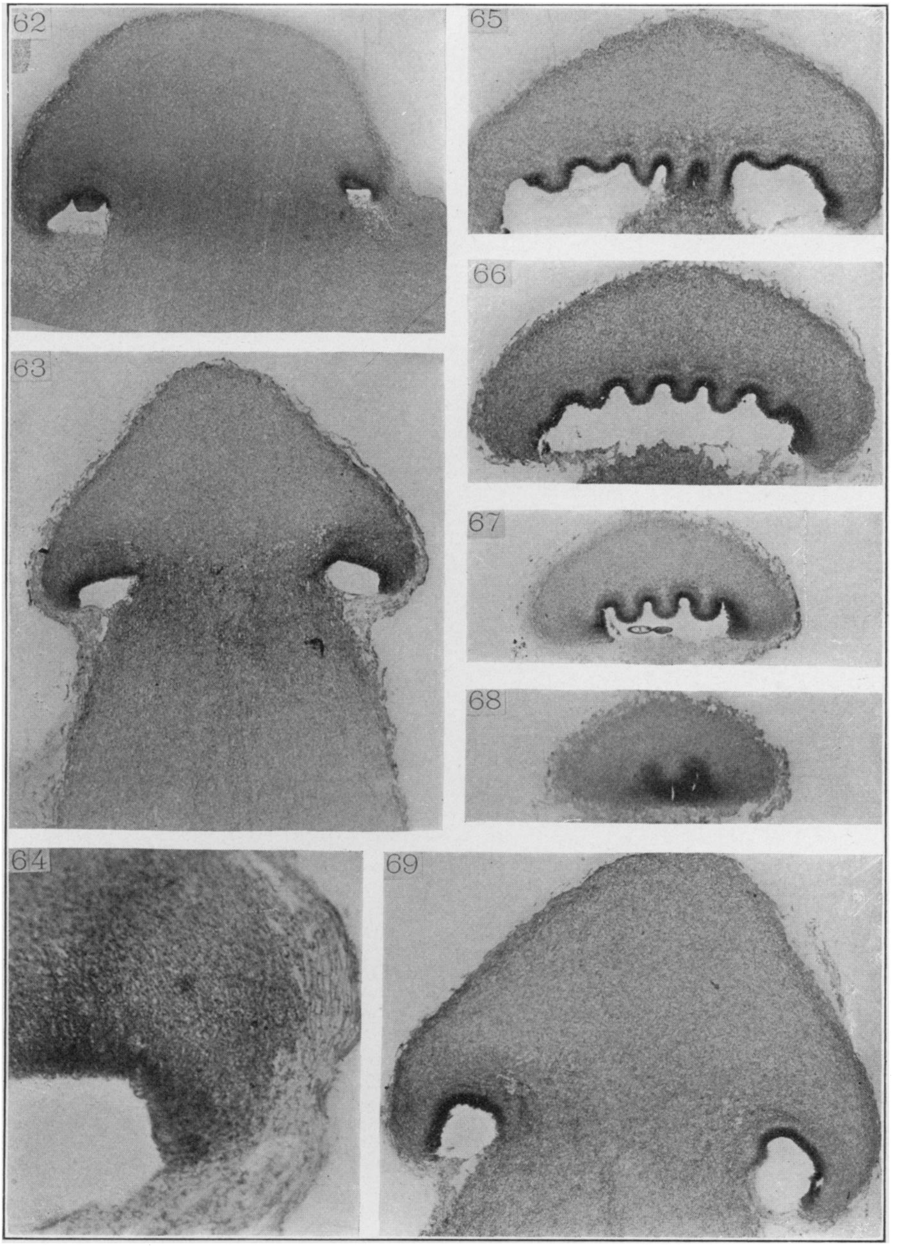
DOUGLAS: CORTINARIUS ARMILLATUS (24); C. CINNAMOMEUS (25–38).



DOUGLAS: CORTINARIUS CINNAMOMEUS.



DOUGLAS: CORTINARIUS LILACINUS.



DOUGLAS: CORTINARIUS LILACINUS (62); C. DISTANS (63–69).